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Authors

Coble, AA
Hart, SC

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The significance of atmospheric nutrient inputs and canopy interception of precipitation during ecosystem development in piñon–juniper woodlands of the southwestern USA

Ashley A. Coble [a,*], Stephen C. Hart [b]

[a] School of Forestry, Northern Arizona University, PO Box 15018, Flagstaff, AZ 86011, USA
[b] Life & Environmental Sciences and the Sierra Nevada Research Institute, University of California, Merced, 5200 North Lake Road Merced, CA 95343, USA

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ABSTRACT

In arid ecosystems, widely spaced vegetation and prolonged dry periods may enhance canopy capture of nutrients from dry deposition. Additionally, differences in precipitation type, plant canopy architecture, and soil nutrient limitation could affect canopy exchange of atmospherically derived nutrients. We collected bulk precipitation and throughfall underneath piñon pine (*Pinus edulis*) and one-seed juniper (*Juniperus monosperma*) along a substrate age gradient to determine if canopy interception or throughfall chemistry differed among tree species, season, or substrate age. The Substrate Age Gradient of Arizona consists of four sites with substrate ages ranging from 1 ky to 3000 ky-old, which exhibit classic variations in soil nitrogen (N) and phosphorus (P) availability with substrate age. Greater nutrient inputs below canopies than in intercanopy areas suggest throughfall contributes to the "islands of fertility" effect. Canopy interception of precipitation did not differ between tree species, but was greater in the summer/fall than winter/spring. We found that net canopy retention of atmospherically derived N was generally greater when N availability in the soil was low, but retention also occurred when N availability was relatively high. Taken together, our results were inconclusive in determining whether the degree of soil nutrient limitation alters canopy exchange of plant growth-limiting nutrients.

1. Introduction

Plant essential nutrients enter terrestrial ecosystems from the atmosphere and by the weathering of parent material. Nitrogen (N) and carbon (C) are predominately supplied by the atmosphere, while phosphorus (P) and so-called base cations (e.g., sodium (Na), potassium (K), calcium (Ca), and magnesium (Mg)) are primarily derived from weathering of residual parent material. However, in some cases, the atmosphere can also contribute significant amounts of these nutrients (Chadwick et al., 1999; Reynolds et al., 2001, 2006). For instance, in an arid region on the Colorado Plateau of the American Southwest, dust may supply P in quantities as great as the contribution of P from bedrock weathering (Reynolds et al., 2001).

During rainfall events, dust particles deposited onto tree canopies are washed from leaf surfaces and are deposited onto the soil beneath the canopy (Parker, 1983). Interception of precipitation by the tree canopy and its transport to the soil surface (i.e., throughfall) alters the chemical composition of precipitation through two key processes: washing of impacted nutrients and exchange of nutrients with the canopy (absorption and leaching). Leaching of nutrients from the interior of foliage occurs via ion replacement reactions between water and exchangeable ions present in the intercellular free space of leaves (Parker, 1983). Similarly, canopy uptake occurs as absorption through cuticles and stomates (Parker, 1983). Whether a nutrient is absorbed or leached varies for each nutrient. For many nutrients, canopy leaching occurs when there are high foliar concentrations of that nutrient in a chemical form and location within the foliage that can easily be removed by water (Parker, 1983; Tukey, 1970). For example, structural elements (e.g., N) are less likely to be leached from foliage than elements in the cell solution (e.g., K; Tukey, 1970).

In humid ecosystems, canopy uptake of nutrients has been reported to be greater for nutrients that are strongly limiting to plant growth. For example, Lindberg et al. (1986) reported significant foliar absorption of NO_3^- and NH_4^+ in a N-deficient deciduous forest ecosystem. However, little is known about the pattern of nutrient uptake by plant canopies in arid ecosystems that vary in soil nutrient availability. A substrate age gradient provides a "natural experiment" (Vitousek, 2005) to examine how throughfall

* Corresponding author. Current address: Department of Biological Sciences, Michigan Technological University, 1400 Townsend Drive, Houghton, MI 49931, USA. Tel.: +1 620 200 7696; fax: +1 906 487 3167.
E-mail address: aacoble@mtu.edu (A.A. Coble).

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chemistry differs with variations in soil N and P availability because the relative availability of these nutrients varies across different stages of ecosystem development. On younger substrates, greater P availability occurs because P is a rock-derived nutrient and weatherable P-containing minerals are relatively abundant in younger substrates; however, over time these minerals are weathered and P is lost from the soil via leaching and surface erosion (Crews et al., 1995; Walker and Syers, 1976). In contrast, N, an atmospherically derived nutrient, is supplied by exogenous inputs to the ecosystem and thus tends to accumulate over time; hence, N is often more available on older than younger substrates (Crews et al., 1995).

There have been few studies of throughfall chemistry in the semi-arid southwestern United States of America (USA). Piñon–juniper woodlands are a major vegetation type in this region (220,000 km^2; Lowry et al., 2007) and dry (i.e., arid and semi-arid) ecosystems occupy approximately 20% of the Earth (Smith et al., 1997). Piñon–juniper woodlands are characterized by widely spaced trees, and because canopies often do not overlap throughfall fluxes can be estimated by species and at the individual tree level. Hart and Parent (1974) suggested that isolated trees may trap more dust because they have completely exposed canopies compared with trees inside forest stands. Due to enhanced dust trapping by tree canopies, measurements of nutrient inputs in throughfall may provide a better estimate of atmospheric nutrient inputs than bulk precipitation (wet and dry deposition collected in a nearby open area) in areas where dust is a major contributor. Throughfall inputs comprised of nutrient contributions from dry deposition, precipitation, and leaching from the canopy can supply important nutrient inputs to soils below the tree and contribute to spatial heterogeneity of soil nutrients often observed in arid regions (e.g., Garner and Steinberger, 1989).

Interception of precipitation by the tree canopy refers to precipitation that is not delivered to the soil surface via throughfall or stemflow, and can alter the water balance in a wide range of forests (Carlyle-Moses, 2004; Owens et al., 2006). Investigating canopy interception is important for understanding hydrological budgets especially in arid and semi-arid areas with highly variable annual precipitation (Sheppard et al., 2002). Precipitation intercepted by the tree canopy can be lost to the atmosphere (via evaporation if rain or sublimation if snow) before the water infiltrates into the soil, effectively reducing the amount of water available to trees and understory plants (Dunkerley and Booth, 1999; Pressland, 1973). Some studies in arid and semi-arid regions (Dunkerley and Booth, 1999; Návar et al., 1999; Slatyer, 1965) suggest the relative magnitude of canopy interception loss compared to precipitation inputs can be as large as in many humid forests, but is highly variable across sites and years. For example, in the southwestern USA alone, interception losses range from 2 to 62% underneath individual trees and shrubs (e.g., Martinez-Meza and Whitford, 1996; Skau, 1964).

In arid and semi-arid ecosystems, investigations of both throughfall chemistry and canopy interception are sparse, and to our knowledge no previous studies in arid environments have investigated whether atmospheric inputs and canopy exchange of limiting nutrients vary with substrate age. In this study, we investigated seasonal and annual water and nutrient inputs in bulk precipitation and throughfall of piñon pine and one-seed juniper along a three million year old semi-arid substrate age gradient (Selmants and Hart, 2008, 2010) to address the following hypotheses: 1) canopy exchange of N and P would vary with substrate age due to changes in soil N and P availability with soil development; 2) the degrees of canopy interception of precipitation would differ between species due to differing leaf morphology and canopy structure of the two co-dominant tree species; and 3) the degree of canopy interception or throughfall chemistry composition would vary seasonally due to seasonal differences in precipitation type and atmospheric water-deficit. Additionally, given the paucity of studies of throughfall chemistry in arid regions, we compared our estimates of bulk precipitation and throughfall with estimates from other arid regions.

2. Methods

2.1. Site description

This study was conducted along the Substrate Age Gradient of Arizona (SAGA; see Selmants and Hart, 2008, 2010 for more details). The SAGA consists of four sites that vary in substrate age: 900 y, 55,000 y, 750,000 y, and 3,000,000 y. The underlying substrate at each of the sites is comprised of basaltic cinders and each of the site locations has minimal slope. The elevations at these four sites range from 1905 m to 2073 m. The vegetation at these sites consists of two co-dominant tree species: piñon pine (*Pinus edulis*) and one-seed juniper (*Juniperus monosperma*). Vegetation in intercanopy spaces consists primarily of blue grama (*Bouteloua gracilis*) at the three oldest sites. At the youngest site, intercanopy spaces contain primarily the shrubs Apache plume (*Fallugia paradoxa*) and skunkbush sumac (*Rhus Trilobata*). The SAGA sites experience similar climate, with a mean annual precipitation of ~340 mm, mean annual temperature of ~11 °C, and prevailing southwesterly winds.

Along the SAGA, experimental nutrient amendments of N, P, and water applied to *Bouteloua gracilis* at three of the study sites (the youngest site was not included in the study) suggested net primary productivity (NPP) at the 55 ky-old site is limited by N and water, NPP at the 750 ky-old site is not limited by N or P, and NPP at the 3000 ky-old site is limited by P; (G. Newman, Northern Arizona University, unpublished data). Additionally, soil N availability increases with substrate age until the 750 ky-old site, and then decreases at the 3000 ky-old site, although N availability is still higher at the 3000 ky-old site than at the two youngest sites (Selmants and Hart, 2008). Phosphorus availability is greatest at the 1 ky-old site and decreases with substrate age (Selmants and Hart, 2010).

2.2. Collection methods

We selected eight one-seed junipers and eight piñon pines within an approximately 1.5 ha area at each of the four sites using the following criteria. All of the trees selected were between 4.5 and 5.0 m tall, had a canopy diameter of approximately 5 m, and had a basal stem diameter between 25 and 35 cm. This tree size is larger than the mean size class (mean piñon basal quadratic diameter = 15.0 cm; mean juniper basal-stem quadratic diameter = 24.6 cm) across the four study sites (Chris Looney, Northern Arizona University, unpublished data). For logistical reasons, we were unable to measure throughfall adequately under trees of both species and across all tree size classes. Therefore, we selected this largest tree-size class to provide an estimate of the amount of canopy interception and throughfall nutrient fluxes across all sites. We also wanted to compare how canopy interception and throughfall varied between tree species; therefore, we selected similarly sized trees to evaluate species effects. Selmants and Hart (2008) previously established 12 intercanopy spaces, selected at random, that were a minimum of 10 m in diameter interspersed through the sites. We randomly selected eight of these at each site for location of our bulk precipitation collectors (see below).

At each site, we placed one throughfall collector underneath eight piñon pine and eight one-seed juniper tree crowns (similar to methods used by Classen et al., 2005). According to Hansen (1996), the quantity of throughfall increases with distance of the throughfall collector from the bole; therefore, we positioned throughfall collectors mid-way between the bole and the crown drip-line as an estimate of mean canopy interception. We randomly assigned collector aspect to one of the four cardinal directions for

each throughfall collector. One bulk precipitation collector was also located in the approximate center of eight different intercanopy spaces at each site.

Bulk and throughfall collectors consisted of a 1-L, high-density polyethylene (HDPE) Nalgene® small mouth bottle, with the narrow opening of an HDPE funnel inserted into the mouth of the bottle and the larger, 150 mm diameter, opening facing up (similar in design to collectors used by Classen et al., 2005). We placed a piece of 1-mm nylon mesh and four glass marbles into the funnel flute to minimize evaporation and to prevent canopy litter from entering the collection bottle. The top of the funnels were oriented perpendicular to the zenith, and the collectors were stabilized by placing them inside a section of 10-cm diameter polyvinyl chloride pipe anchored to the ground with rebar. Prior to deployment, the bottles and funnels were acid washed (0.5 M HCl) and rinsed well with deionized water. The marbles and nylon mesh were also rinsed with deionized water prior to deployment.

Samples were collected within a week of each precipitation event. There were a total of 10 winter/spring precipitation events (December 1, 2008 to May 31, 2009) and 11 summer/fall precipitation events (June 1, 2009 to November 30, 2009) for a total of 21 collections over the one year period (December 1, 2008 until November 30, 2009). The 750 ky-old site was inaccessible during a winter storm in December of 2008, and thus no samples were collected from that site for that particular precipitation event. Because a weather station equipped with an unheated, tipping bucket rain gauge was installed at each site, we were able to estimate the amount of precipitation missed from this event in order to calculate annual precipitation from the bulk precipitation collector (see below). However, we cannot account for the missed amount of nutrient inputs in bulk precipitation and throughfall that occurred during this event, which comprised 23% of total winter precipitation at this site. Hence, nutrient fluxes from the 750 ky-old site are underestimated, but this uncollected precipitation event does not affect comparisons of throughfall between tree species at this site.

After each collection, we weighed each sample and converted it into volume assuming a water density of 1 Mg m^{-3}. The amount of precipitation or throughfall (cm) in each collector was determined by dividing this volume by the cross sectional funnel area. At each site, the fraction of canopy interception for each tree species was calculated as: (mean intercanopy precipitation − canopy throughfall)/mean intercanopy precipitation; Classen et al., 2005). Weather stations containing an unheated tipping bucket rain gauge (Texas Electronics, Dallas, TX, USA) monitored precipitation events at each site. These data were used to evaluate the efficiency of bulk precipitation collectors relative to this type of rain gauge, which is frequently used to measure precipitation in reporting weather stations.

2.3. Laboratory methods

For chemical analyses, bulk precipitation and throughfall samples from different collection periods were composited by season on a mass-weighted basis. We divided the collections into two seasons: winter/spring (primarily snow) and summer/fall (primarily monsoonal rains) to reflect the different types of precipitation events characteristic of the region. The summer/fall collections will hereafter be referred to as summer and the winter/spring collections will be referred to as winter collections. Samples were kept frozen until analyzed.

We analyzed all throughfall and bulk precipitation samples for the following cations and anions using ion chromatography (Dionex DX 500 Ion Chromatograph, Sunnyvale, CA, USA): ammonium (NH_4^+), sodium (Na^+), potassium (K^+), calcium (Ca^{2+}), magnesium (Mg^{2+}), nitrate (NO_3^-), nitrite (NO_2^-), chloride (Cl^-), sulfate (SO_4^{2-}), and phosphate (PO_4^{3-}). Samples were introduced to the analyzer through 20 μm polyethylene membrane filter caps. For anion analysis, samples were eluted with 1.8 mM sodium carbonate and 1.7 mM sodium bicarbonate run through an IonPac AS4A-SC 4 × 250 mm analytical column with a Dionex ASRS-Ultra 4 mm anion self-regenerating suppressor. For cation analysis, samples were eluted with 20 mM methanesulfonic acid and run through a CS12A 4 × 250 mm analytical column with a CSRS-Ultra II 4 mm cation self-regenerating suppressor. We also analyzed all samples for total N and P by Kjeldahl digestion of 20-ml aliquots, using a digestion procedure similar to that described by Haubensak et al. (2002) for 0.5 M K_2SO_4 extracts of soil. Total N and P (modified from Lachat QuikChem® methods 10-107-06-2-E and 13-115-01-1-B, respectively) were measured in digestates using a Lachat Instruments QuickChem® 8000 Flow Injection Analyzer (Lachat Instruments, Loveland, Colorado, USA). Prior to analysis, composited samples were filtered through a 20-μm ashless cellulose filter paper (Whatman 41) that had been preleached with deionized water. Analyses returned values below detection limits for several elements, and the detection limits for those elements were as follows: PO_4^{3-} = 0.01 mg P L^{-1}; NO_2^- = 0.01 mg N L^{-1}; SO_4^{2-} = 0.01 mg S L^{-1}; total P = 0.03 mg P L^{-1}, and total N = 0.12 mg N L^{-1}. Organic N was calculated by subtracting NH_4^+–N from total N. We have presented our nutrient data as a flux (mg m^{-2} y^{-1} or mg m^{-2} $season^{-1}$) rather than as a concentration (mg L^{-1}). However, linear regressions of data from all collectors, seasons, and sites revealed a significant ($p < 0.05$) positive relationship between concentration and flux of each mineral element (NH_4^+: $r^2 = 0.697$; Na^+: $r^2 = 0.410$; K^+: $r^2 = 0.573$; Ca^{2+}: $r^2 = 0.460$; Mg^{2+}: $r^2 = 0.462$; NO_3^-: $r^2 = 0.624$; Cl^-: $r^2 = 0.288$; SO_4^{2-}: $r^2 = 0.494$; Organic N: $r^2 = 0.490$; $n = 192$ for all elements).

2.4. Statistical analyses

Unheated, tipping bucket rain gauge measurements were compared with measurements from bulk precipitation collectors from all sites and all collection dates when rain gauges were operational. Least-squares, linear regression showed that bulk precipitation was well correlated to precipitation measured using the tipping bucket rain gauge (data pooled across sites and collection dates; bulk precipitation (mm) = 0.91 × rain gauge precipitation + 0.04; $r^2 = 0.954$; $n = 48$; $p < 0.01$). Bulk precipitation and rain gauge values from the 750 ky-old site were significantly correlated (all collection dates when the rain gauge was operational; bulk precipitation (mm) = 0.96 × rain gauge precipitation − 1.15; $r^2 = 0.971$; $n = 15$; $p < 0.01$). We used this equation to predict the amount of bulk precipitation that would have been collected from the missed winter collection event, and this value was incorporated in the annual precipitation estimate for the 750 ky-old site. Because of power losses and data storage malfunctions, precipitation data from weather stations were missing during the study period for 199 days from the 1 ky-old site, 328 days from the 55 ky-old site, and 65 days from the 750 ky-old site; no precipitation data were missing from the 3000 ky-old site.

We used a two way analysis of variance (ANOVA) to determine if season, collector location, or their interactions significantly influenced canopy interception of precipitation. For this analysis, we used site as a replicating factor ($n = 4$) because similar sized trees of piñon and juniper were used at all sites; hence, there was no *a priori* reason to expect a site effect on canopy interception. Our sampling design also did not pair throughfall collectors with bulk precipitation collectors in a way that would allow within-site replication. We estimated the percent interception at an ecosystem scale by multiplying the proportion of canopy cover by species at each site (C. Looney, Northern Arizona University, unpublished data) by the species and site specific values. We acknowledge that our canopy interception data are derived from a single size class of trees and that

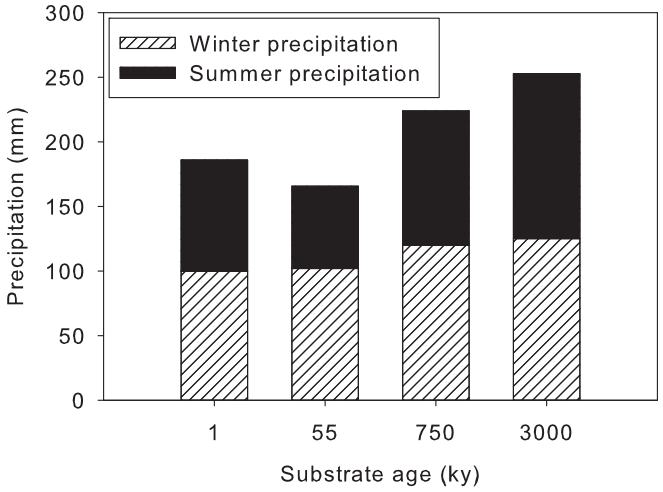

Fig. 1. Seasonal precipitation collected in bulk precipitation collectors from December 2008 through November 2009 along the Substrate Age Gradient of Arizona (SAGA). Winter collections: December 1, 2008 to May 30, 2009; Summer collections: June 1, 2009 to November 30, 2009. Along the SAGA, mean annual precipitation between 2002 and 2005 was 328–352 mm (measured with unheated, tipping bucket rain gauges placed at each site).

size class is larger than mean and median size classes at each site, which may affect overall ecosystem scale estimates. These estimates also neglect interception of two species of shrubs that dominate intercanopy spaces at the youngest site, as well as canopy interception losses from bunchgrasses that dominate the intercanopy spaces at the three older sites. Nevertheless, we feel that the scaling of our data to the ecosystem level is still useful for relative comparisons of canopy interception among other ecosystems given the paucity of data from semi-arid woodlands.

The use of inferential statistics is limited to within-site comparisons because there is no replication at the site level. We used a two-way repeated measures multivariate analysis of variance (RM MANOVA) with season as the repeated factor to test for significant differences between sampling location and season, and their interactions on throughfall chemistry. When RM MANOVAs revealed a significant sampling location and season interaction, we ran a one-way ANOVA of sampling location for each season independently to determine differences among means. Statistical analyses were conducted using JMP 8.0.1 (SAS Institute, Incorporation, Cary, North Carolina). Statistical significance was set *a priori* at $\alpha < 0.05$ for all statistical analyses.

3. Results

3.1. Quantity of precipitation across SAGA

In general, the summer monsoon provides roughly 50% of the total annual rainfall in Arizona (Sheppard et al., 2002), but three of the four sites received less than 50% of total precipitation during the summer of 2009 (Fig. 1). Total precipitation measured with bulk precipitation collectors during the 365 days of this study was much lower than the mean annual precipitation for each site (Fig. 1).

3.2. Effect of sampling location and season on limiting nutrients across SAGA

Canopy exchange of NH_4^+–N, defined as throughfall minus bulk precipitation NH_4^+–N fluxes, varied across the SAGA with canopy uptake of NH_4^+–N (i.e., bulk precipitation fluxes greater than throughfall) observed at the youngest and oldest sites and canopy leaching of NH_4^+–N observed at the intermediately-aged sites (i.e.

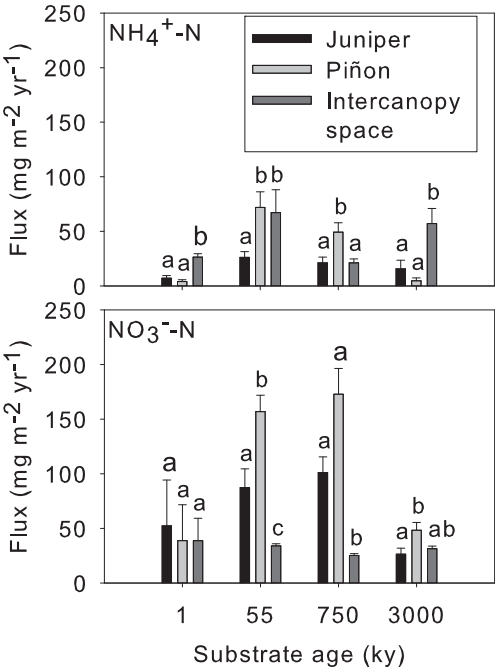

Fig. 2. Influence of sampling location (under piñon canopy, under juniper canopy, intercanopy space = bulk precipitation) on inorganic nitrogen inputs from the atmosphere along the Substrate Age Gradient of Arizona (SAGA). Different lower case letters above bars indicate the sampling location means differ significantly for that nutrient ($p < 0.05$), determined with one-way ANOVA and Tukey's HSD. Error bars represent ± one standard error of the mean ($n = 8$).

bulk precipitation fluxes less than throughfall; Fig. 2). At the 1 ky-old and 3000 ky-old sites, NH_4^+–N fluxes were significantly greater in intercanopy spaces than underneath canopies, and at the 55 ky-old site NH_4^+–N fluxes were significantly greater in intercanopy spaces and below piñon canopies than below junipers (Fig. 2). At the 750 ky-old site, winter fluxes of NH_4^+–N did not differ among sampling location, but summer NH_4^+–N fluxes were significantly greater underneath piñons than under junipers or in intercanopy spaces (Fig. 2).

Canopy leaching of NO_3^- was observed at the 55 ky-old and 750 ky-old sites (Fig. 2). At the 55 ky-old site, there was a significant interaction of season and sampling location for NO_3^- (Table 1). In the winter, NO_3^- fluxes were greater under piñons than junipers and greater under junipers than in intercanopy spaces. Summer NO_3^- fluxes were similar between tree species, but greater beneath canopies than in intercanopy spaces (Table 1). At the two oldest sites there were significant effects of sampling location for NO_3^-; NO_3^- fluxes were greater underneath canopies at the 750 ky-old site than in intercanopy spaces, and NO_3^- fluxes at the 3000 ky-old site were greater underneath piñons than junipers. Analysis of inorganic N fluxes summed together (NH_4^+ and NO_3^-) revealed similar patterns as described for NH_4^+–N (data not shown). A seasonal effect of NO_3^- fluxes was observed at only one of the four sites, and no seasonal effects were observed for NH_4^+ (Table 1). Organic N was the only constituent whose fluxes did not differ among sampling locations and sites, or between seasons (data not shown; 0–134 mg m^{-2} y^{-1} across sites and sampling locations). Inputs as bulk precipitation or throughfall of PO_4^{3-}–P, Total P, and NO_2–N were below detection limits for all sampling locations.

3.3. Effect of sampling location and season on other nutrients across SAGA

Potassium fluxes were significantly greater beneath canopies than in bulk precipitation (Table 2). All significant sampling

Table 1
Mineral elements (mg m^{-2} $season^{-1}$) in juniper and piñon throughfall and bulk precipitation sampling locations collected from December 1, 2008 to May 30, 2009 (Winter), and from June 1, 2009 to November 30, 2009 (Summer) across all sites (1 ky-old, 55 ky-old, 750 ky-old, 3000 ky-old). Significant ($p < 0.05$) seasonal effects and sampling location effects are denoted by different lower case letters following their means and significant interactions of season × sampling location are denoted with an asterisk (*). Statistical significance within each site was determined with repeated measures multivariate analysis of variance (ANOVA). Where significant season × sampling location interactions occurred, means that are followed by different lower case letters differ significantly as determined by one way ANOVA within each season.[a] The following nutrients were below our detection limits: PO_4^{3-}, total P, and NO_2^-.

	NH_4^+–N	Na^+	K^+	Ca^{2+}	Mg^{2+}	NO_3^-–N	Cl^-
1 ky-old substrate							
Interaction				*	*		
Winter	9.4	43.3	133	256 a	31.4 a	43.0 a	58.0 a
Juniper	4.6 a	47.3 a	247 a	491 a	39.1 a	52.1 a	76.0 a
Piñon	3.5 a	51.5 a	135 a	193 b	44.9 a	51.1 a	49.6 ab
Intercanopy space	19.9 b	31.2 a	18.0 b	85.0 c	10.2 b	25.9 a	18.5 b
Summer	15.8	40.6	245	294 b	40.8 b	43.7 b	86.4 b
Juniper	9.8 a	38.3 a	387 a	474 a	50.0 a	52.5 a	116 a
Piñon	4.6 a	40.2 a	321 a	168 b	44.7 a	26.6 a	83.9 b
Intercanopy space	33.0 b	43.2 a	27.0 b	240 b	27.3 a	51.9 a	59.5 b
55 ky-old substrate							
Interaction				*	*	*	*
Winter	49.7	80.6 a	220	341	52.7	103	173
Juniper	32.7 a	79.4 a	372 a	628 a	67.8 a	100 a	199 a
Piñon	80.5 b	122 b	254 a	291 b	75.5 a	180 b	164 a
Intercanopy space	36.0 b	39.9 a	33.9 b	104 c	14.8 b	28.7 c	157 a
Summer	60.6	55.2 b	231	289	54.3	82.7	117
Juniper	19.8 a	40.6 a	286 a	391 a	57.3 ab	75.0 a	140 a
Piñon	63.5 b	84.2 b	313 a	258 a	72.5 a	134 a	141 a
Intercanopy space	98.5 b	40.7 a	94.9 b	219 a	33.1 b	39.6 b	71.6 b
750 ky-old substrate							
Interaction	*	*		*	*		*
Winter	28.6	75.7	131 a	271	38.7	92.5	145
Juniper	21.1 a	76.8 a	167 a	407 a	36.8 a	79.9 a	134 a
Piñon	35.2 a	117 a	187 a	316 a	72.4 b	177 a	166 a
Intercanopy space	30.7 a	32.8 b	35.7 b	69.9 b	7.18 c	22.4 b	137 a
Summer	32.3	63.5	215 b	443	64.2	106	128
Juniper	21.4 a	60.8 a	284 a	592 a	68.8 a	123 a	140 a
Piñon	63.6 b	92.7 b	311 a	429 b	95.7 a	169 a	165 a
Intercanopy space	12.0 a	37.1 c	49.4 b	308 c	28.1 b	27.9 b	79.8 b
3000 ky-old substrate							
Interaction							
Winter	17.3	75.7	131 a	271 a	38.7 a	38.7	145 a
Juniper	8.1 a	61.0 a	203 a	503 a	38.1 a	32.4 a	76.6 a
Piñon	0.5 a	71.4 a	168 a	183 b	42.9 a	53.5 b	106 a
Intercanopy space	58.9 b	36.6 a	58.7 b	98.5 b	10.5 b	25.0 ab	57.1 a
Summer	29.5	36.5	215 b	443 b	64.2 b	33.9	129 b
Juniper	23.6 a	31.8 a	348 a	682 a	65.9 a	20.4 a	137 a
Piñon	9.3 a	40.5 a	480 a	233 b	63.9 a	43.2 b	105 a
Intercanopy space	55.7 b	34.6 a	97.4 b	194 b	33.5 b	38.0 ab	115 a

[a] Detection limits were as follows: NH_4^+: 0.36 mg N m^{-2} y^{-1}; NO_3^-: 0.36 mg N m^{-2} y^{-1}.

location effects of other nutrients (i.e., Cl^-, Na^+, Mg^{2+}, Ca^{2+}) were observed at only one site (Table 1). At the two intermediate aged sites, there were significant interactions of season and sampling location for Cl^-, and at the 750 ky-old site there was also a significant interaction for Na^+ (Table 1).

At the three younger sites, Ca^{2+} and Mg^{2+} fluxes behaved similarly, with variations in nutrient fluxes dependent on both season and sampling location (Table 1). At the oldest site, Ca^{2+} and Mg^{2+} fluxes were greater in summer than winter and the sampling location also differed significantly; no significant interaction occurred with season for either nutrient. At the three younger sites, significant interactions among season and sampling location occurred; winter Ca^{2+} fluxes were greater under junipers in the winter than intercanopy spaces, and were often greater than below piñons. Summer fluxes of Ca^{2+} were more variable than winter fluxes among these sites (Table 1). Winter Mg^{2+} fluxes were greater underneath canopies than intercanopy spaces and, at the 750 ky-old site, Mg^{2+} fluxes differed among all sampling locations (Table 1). Summer fluxes of Mg^{2+} were more variable than winter fluxes among sites (Table 1).

There were no seasonal effects of throughfall chemistry that were observed consistently across all four sites, and only two nutrients, K^+ and Cl^-, had significant seasonal effects at more than one site (Table 1). Sulfate fluxes at the 3000 ky-old site were greater in the winter than the summer (data not shown). All other seasonal (Na^+, Ca^{2+}, and Mg^{2+}) effects of nutrients were observed at only one of the four sites (Table 1).

3.4. Annual nutrient contributions of throughfall and bulk precipitation across sites

Across the substrate age gradient on an annual basis, Ca^+ in throughfall was often enriched relative to bulk precipitation across the substrate age gradient, particularly underneath juniper canopies (data not shown). Magnesium and K^+ were always enriched in throughfall relative to bulk precipitation (data not shown). Other elements had variable differences between tree species among the sites (data not shown).

There were some differences of nutrient flux in bulk precipitation across sites. Differences in nutrient inputs in bulk precipitation were driven by differences in the amount of precipitation across sites, not by differences in nutrient concentrations (data not shown). Nutrient flux in bulk precipitation varied among sites for NH_4^+, but NO_3^- fluxes were similar among sites (Fig. 2). Ammonium input in bulk precipitation was greater at the 55 ky-old site (67 mg N m^{-2} y^{-1}) and the 3000 ky-old site (57 mg N m^{-2} y^{-1}) than at the 750 ky-old site (21 mg N m^{-2} y^{-1}). Potassium inputs were greater at the 55 ky-old (64 mg m^{-2} y^{-1}) and 3000 ky-old sites (78 mg m^{-2} y^{-1}) than at the 1 ky-old site (23 mg m^{-2} y^{-1}). Sulfate inputs in bulk precipitation were also greater at the 55 ky-old site (22 mg S m^{-2} y^{-1}) and the 3000 ky-old site (18 mg S m^{-2} y^{-1}) than at the 750 ky-old site (12 mg S m^{-2} y^{-1}).

3.5. Canopy interception of precipitation among tree species and seasons

The degree of canopy interception was similar among tree species (Table 2). Across the SAGA, canopy interception losses ranged from 43.2% to 65.9% in the summer and from 35.6% to 46.6% in the winter season. Annual interception losses ranged from 40.9% to 56.2% (Table 2). Canopy interception scaled to the ecosystem level ranged from 10.3% to 25.0% in the summer and 7.0%–17.4% in the winter across the SAGA. Annual ecosystem scale interception estimates ranged from 8.6% to 21.2% across the SAGA (Table 2). Canopy interception differed among seasons with significantly more precipitation intercepted by tree canopies in the summer than during the winter (Table 2).

4. Discussion

4.1. Nutrient limitations and throughfall chemistry

Few studies have investigated both throughfall chemistry and canopy interception in arid and semi-arid ecosystems, and to our knowledge this is the first study to investigate how atmospheric inputs and canopy exchange of limiting nutrients vary with substrate age in arid environments. In a previously studied humid

Table 2
Seasonal and annual percent (%) interception by juniper and piñon canopies along the Substrate Age Gradient of Arizona (SAGA) measured under individual tree canopies and extrapolated to the ecosystem-scale. Ecosystem-scale estimates were derived using the percentage of canopy cover (projected area) of each tree species at each site.

Substrate age (ky)	One-seed Juniper				Piñon-pine				Ecosystem-scale		
	Winter	Summer	Annual	Canopy cover	Winter	Summer	Annual	Canopy cover	Winter	Summer	Annual
1	53.4	69.4	61.4	4.5	39.8	62.3	51.1	11.5	7.0	10.3	8.6
55	48.2	63.6	55.9	13.1	35.0	60.0	47.5	5.3	8.2	11.5	9.8
750	43.0	50.7	46.8	20.9	34.2	35.7	35.0	2.3	9.8	11.4	10.6
3000	37.5	50.4	43.9	33.1	33.8	56.5	45.2	14.7	17.4	25.0	21.2
Mean	45.5	58.5	52.0	17.9	36.7	53.6	44.7	8.5	10.6	14.5	12.6

forest, net canopy uptake of N occurred when the availability of N was low in the soil and limiting to plant growth (Lindberg et al., 1986). Additionally, experimental applications of N fertilizer to black spruce stands revealed higher concentrations of total N in throughfall below canopies on N fertilized plots relative to control plots (Mahendrappa and Ogden, 1973). Hence, we hypothesized that along the SAGA, net canopy uptake of N would occur in younger soils where N was limiting, and net canopy uptake of P would occur in the older soils where P was limiting (Selmants and Hart, 2008, 2010). Consistent with this hypothesis, canopy uptake of NH_4^+ occurred in both co-dominant tree species at the youngest and most N-limited site, and no canopy uptake (juniper) or canopy leaching of NH_4^+ (piñon) occurred at the 750 ky-old site (Fig. 2) where soil N availability is highest (Selmants and Hart, 2008). Inconsistent with this hypothesis, canopy uptake of NH_4^+also occurred in junipers at the 55 ky-old and 3000 ky-old sites where soil N availability is intermediate (Selmants and Hart, 2008). Furthermore, the capacity of junipers and piñon trees to take up NO_3^- appears limited as both of these species either showed no canopy uptake of NO_3^- (1 and 3000 ky-old sites) or net canopy leaching of NO_3^- (55 and 750 ky-old sites). Our data suggests large NO_3^- losses from the canopy can occur, and these losses are of greater magnitude than any observed NH_4^+ uptake. Hence, even if trees can respond to reduced soil N availability by taking up more NH_4^+ then these trees may lose more N than they gain from atmospheric inputs. Despite a strong gradient in P availability across the SAGA (Selmants and Hart, 2010), we were unable to detect inorganic or total P inputs in throughfall or bulk precipitation at any of these sites, and therefore we were unable to determine whether canopy uptake of P from atmospheric sources, if it occurs, covaries with soil P availability across these sites.

Studies in arid ecosystems along the central Colorado Plateau have reported considerable dust contributions of P to surficial (upper 5 cm) soils, essentially doubling the soil total P relative to that stored in bedrock over decadal or longer timescales (Reynolds et al., 2001, 2006). Contemporary estimates of P inputs as dust deposited on snow (~3500 m elevation) in the nearby San Juan Mountains of southwestern Colorado, USA, were 4.54 mg m^{-2} yr^{-1} (Lawrence et al., 2010), a significant P input to these ecosystems if maintained over similar long time periods. We found that contemporary inputs of dissolved inorganic PO_4^{3-}–P and total (dissolved and particulate < 20 μm) P in throughfall and bulk precipitation across the SAGA on the southern Colorado Plateau were below our detection limits (1.4 mg PO_4^{3-}–P m^{-2} y^{-1} and 4.1 mg total P m^{-2} y^{-1}, assuming an annual water flux of 136 mm, the mean annual flux among collectors and study sites). Annual fluxes of P observed by Lawrence et al. (2010), if all this P was in soluble and fine particulate forms, would be only be marginally detected as total P using our methods. However, significant P may be also entering these ecosystems as insoluble, coarse (>20 μm) aerosols (e.g., in soil minerals such as apatite), as our analytical methods did not measure these potential inputs of P. Using measured annual dust fluxes from the SAGA sites (mean = 8 g m^{-2} y^{-1}; Emerson, 2010), which were collected concurrently with this study, and assuming dust P concentrations are similar between the San Juan Mountains (0.91 mg P g^{-1}; Lawrence et al., 2010) and the SAGA, we estimate total particulate P inputs as dust at the SAGA of 7.2 mg P m^{-2} y^{-1}. This estimate of P flux in dust is of similar magnitude to fluxes reported in the San Juan Mountains, and could provide a significant input of P to these ecosystems over time.

In the only other study of changes in throughfall nutrient inputs along a soil chronosequence (80–~500 ky-old marine terraces in humid coastal Oregon), Bockheim and Langley-Turnbaugh (1997) reported that only one of their five study sites had a mean NO_3^- concentration in throughfall less than in bulk precipitation (NH_4^+ and total N were not measured). Furthermore, PO_4^{3-} inputs were undetectable in throughfall and bulk precipitation across their sites. Assuming that soil N and P availability varied significantly across this highly weathered substrate age gradient, their data suggest that canopy uptake of soil-limiting nutrients does not covary with availability of these nutrients in soil. Taken together, our results from semi-arid woodlands and those from humid forests provide at best only modest support for the hypothesis that soil availability of limiting nutrients influences canopy uptake of atmospherically derived nutrients.

4.2. Throughfall contributions to soil nutrient pools

The "islands of fertility" effect documented in arid and semi-arid regions refers to elevated nutrient contents in soils beneath shrubs or tree canopies compared to soils in intercanopy spaces (Aguiar and Sala, 1999; Schlesinger et al., 1990). Litterfall and domestic livestock grazing are generally identified as the major contributors to this phenomenon because litterfall increases nutrient supply below canopies, and domestic livestock grazing decreases vegetation cover and promotes wind and water erosion in intercanopy spaces (Aguiar and Sala, 1999; Schlesinger et al., 1990). However, in dry regions of the southwestern USA, dust aerosols impacted on isolated plant canopies during dry periods are "washed" from these surfaces following significant precipitation events; these atmospherically derived nutrients can also contribute significantly to enhanced nutrient contents in soils below the plant canopy (Garner and Steinberger, 1989; Hart and Parent, 1974; Klemmedson et al., 1983). For instance, Wezel et al. (2000) argued dust deposition was a contributor to "islands of fertility" for some nutrients in a semi-arid region of Niger. However, Shachak and Lovett (1998) found fine particulate dust contributions were similar beneath shrubs and in inter-shrub spaces in the Negev Desert of Israel, suggesting airborne dust does not consistently contribute to higher nutrient levels in soils beneath plant canopies. Whether or not dust deposition contributes to "islands of fertility" likely depends on differences in erosion and runoff from soils beneath canopies versus soils in intercanopy spaces.

Elevated inputs of Ca^{2+}, Mg^{2+}, and K^+ in throughfall relative to bulk precipitation have been used as indicators of dust deposition (Gorham, 1961; Gosz, 1975; Lindberg et al., 1986). As has been observed in previous studies in other semi-arid regions of the southwestern USA (Gosz, 1975; Hart and Parent, 1974; Klemmedson et al., 1983), we found elevated annual fluxes of these nutrients beneath tree canopies compared to open areas across the SAGA. For instance, annual throughfall fluxes of Ca^{2+}, Mg^{2+}, and K^+ averaged

3.0, 3.6, and 6.8 times higher, respectively, than fluxes in open areas (i.e., bulk precipitation). Our methods do not allow us to distinguish between nutrient contributions from canopy leaching versus deposition, and it is likely both contribute to the high inputs of cations to soils below the canopies across the SAGA. Nevertheless, our results suggest that throughfall augments the "islands of fertility" effect observed in dry ecosystems.

4.3. Regional comparisons of nutrient deposition

This study encompassed only one year, but comparisons of bulk precipitation with regional precipitation data from the National Atmospheric Deposition Program (NADP; http://nadp.sws.uiuc.edu) confirm our data are generally representative of other years regionally (Appendix Tables A1 and A2). The SAGA annual nutrient fluxes in bulk precipitation were often higher than mean annual values (spanning ~28 years) recorded in regional NADP sites, which can be explained, at least in part, by the exclusion of dry deposition from NADP's wet deposition collectors but not our bulk precipitation collectors. Inorganic N fluxes were predominantly in the form of NH_4^+ across the SAGA and NO_3^- at the Grand Canyon NADP site (Appendix Table A1). Furthermore, total N (inorganic + organic N) values in bulk precipitation across the SAGA (mean = 283 mg N m^{-2} y^{-1}, range = 176–406 mg N m^{-2} y^{-1}) were similar to previous measurements of bulk precipitation collected near our study sites, but at a slightly higher elevation (~100 m) adjacent to ponderosa pine (*Pinus ponderosa*) forests (293 mg N m^{-2} y^{-1}, Brown, 1978; 339 mg N m^{-2} y^{-1}, Klemmedson et al., 1983). Clearly, the SAGA receives some of the lowest rates of N deposition in the USA (http://nadp.sws.uiuc.edu), consistent with other regional estimates, and with their great distances from sources of atmospheric N emissions (e.g., industrial and large urban centers).

4.4. Canopy interception of precipitation: species and seasonal effects

The open stand structure of piñon–juniper woodlands allowed us to quantify canopy interception of individual trees rather than at the stand level, the scale used in most studies of canopy interception. Surprisingly, despite the contrasting leaf morphology and canopy structure of piñon and juniper, canopy interception was similar between these two species for trees of similar basal stem diameters. Based on specific leaf area estimates and species-specific allometric equations developed by Grier et al. (1992) near our study sites, we estimate that the projected leaf area of piñon trees were two to three times higher than juniper trees within the range of basal diameters used in our study. Apparently, the canopy architecture or scale-based leaf morphology of juniper offsets the greater leaf area of piñon pine such that canopy interception was similar between these two species for similarly sized individuals.

Previous research conducted at the 1 ky-old site suggests the degree of canopy interception of precipitation is likely affected by canopy architecture. Classen et al. (2005) found that insect herbivory can alter the canopy architecture of piñon pine trees at the 1 ky-old site, causing a reduction in canopy interception of precipitation of 30–50% relative to herbivore-resistant trees and trees where herbivores had been removed experimentally. For one of the herbivores (a stem-boring moth, *Dioryctria albovittella*), a reduction in canopy interception occurred even though no change in leaf area was observed due to herbivory, suggesting that herbivore-driven changes in canopy architecture also contributed to these reductions in canopy interception (Classen et al., 2005). Other studies in arid ecosystems have found inconsistent effects of plant species on canopy interception of precipitation. Návar and Bryan (1990) reported comparable canopy interception of precipitation among species of shrubs in a subhumid subtropical region of Mexico (mean annual precipitation = 740 mm). Martinez-Meza and Whitford (1996) found differences in canopy interception among some species of shrubs but not others in southern New Mexico, USA. They also hypothesized that any differences in canopy interception observed was due to contrasting canopy architecture between species. Clearly, species differences in canopy interception occur in arid and semi-arid environments and are likely driven to a large degree by interspecific differences in canopy architecture. Our data and others (i.e., Classen et al., 2005) suggest that leaf area estimates alone are not good predictors of canopy interception in arid environments, and that other species-specific traits such as leaf morphology and canopy architecture need to be considered when estimating this important hydrologic loss in these ecosystems.

Although plant canopy cover in arid and semi-arid woodlands is less extensive than in humid forests, some studies have estimated precipitation losses to interception can be as great as forest stands (Dunkerley and Booth, 1999; Návar et al., 1999; Slatyer, 1965). Our ecosystem-scale estimates (8.6–21.2%; Table 2) show canopy interception losses in semi-arid piñon–juniper woodlands are comparable to temperate deciduous forests (9.7–20% interception; Carlyle-Moses, 2004) and other studies in semi-arid regions that measured interception losses at the ecosystem scale (e.g., 18.5% and 13.0% in *Larrea tridentata* (Whitford et al., 1997) and *Acacia aneura* (Pressland, 1973) dominated ecosystems, respectively). We likely overestimated ecosystem-scale interception because we used trees within the largest size-class, and hence the most vertically developed canopies, at each site. Furthermore, we did not include stemflow in our estimates of canopy interception, which also could inflate our estimates of canopy interception (Carlyle-Moses, 2004; Hamilton and Rowe, 1949). However, previous studies have reported low stemflow fluxes (<6% of total precipitation) under similar tree species (Owens et al., 2006; Skau, 1964). Taken together, these results suggest that our ecosystem-scale estimates of canopy interception across the SAGA are reasonable.

We found generally higher amounts of canopy interception in the summer than in the winter across the SAGA, suggesting greater interception of precipitation as rain than snow occur in these woodlands. However, these seasonal differences in the degree of canopy interception may also be attributed to differences in evaporative demand of the atmosphere, as well as other factors (i.e., size of precipitation event or precipitation angle; Slatyer, 1965; Rowe, 1983; Crockford and Richardson, 1990a,b). Regardless of whether differences in precipitation type or evaporative demand account for the higher canopy interception in the summer than winter we observed, our results suggest that greater canopy interception of precipitation may occur in these water-limited ecosystems as the climate warms, potentially exacerbating the negative impact of warmer temperatures on soil water availability in the rooting zone of these co-dominant trees. Lower soil water availability coupled with warmer air temperatures have been indicated as causal factors for recent widespread mortality events in piñon–juniper woodlands throughout the southwestern USA (Breshears et al., 2005); increases in canopy interception loss with global warming due to changes in precipitation type may also contribute to these mortality events.

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Appendix

Table A1
Comparisons of mean annual precipitation (MAP) and inorganic nitrogen (N; g m^{-2} y^{-1}) in bulk precipitation at the Substrate Age Gradient of Arizona (SAGA) and wet deposition at nearby regional National Atmospheric Deposition Program sites.

Site	Elevation (m)	Distance from SAGA (km)	MAP[a] (mm)	NO_3^-–N (g m^{-2} y^{-1})	NH_4^+–N (g m^{-2} y^{-1})	Inorganic N (g m^{-2} y^{-1})	Percent as NO_3^-–N
Wet deposition							
Grand Canyon National Park	2152	70–110	368	0.070	0.042	0.112	62.2
Bryce Canyon National Park	2477	230–270	368	0.069	0.043	0.111	61.6
Bandelier National Monument	1998	470–530	393	0.078	0.053	0.131	59.6
Mesa Verde National Park	2172	330–380	425	0.095	0.048	0.143	66.3
Bulk precipitation							
SAGA	1905–2073	–	328–352	0.049–0.068	0.039–0.135	0.088–0.203	33.7–55.9

[a] Mean annual precipitation data based on unheated, tipping bucket rain gauges placed at each site and include years of record from 2002 to 2005.

Table A2
Comparisons of nutrients (g m^{-2} y^{-1}) in bulk precipitation at the Substrate Age Gradient of Arizona (SAGA) and wet deposition at nearby regional National Atmospheric Deposition Program sites.[a]

Site	Element					
	Na^+	K^+	Ca^{2+}	Mg^{2+}	Cl^-	SO_4^{2-}–S
Wet deposition						
Grand Canyon National Park	0.029	0.007	0.095	0.017	0.043	0.074
Bryce Canyon National Park	0.024	0.011	0.079	0.016	0.039	0.070
Bandelier National Monument	0.021	0.010	0.091	0.008	0.032	0.099
Mesa Verde National Park	0.026	0.009	0.167	0.016	0.037	0.139
Bulk precipitation						
SAGA	0.057–0.081	0.045–0.134	0.255–0.369	0.034–0.048	0.108–0.228	0.021–0.044

[a] See Appendix Table A1 for regional site characteristics.

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